Main prey and predators of redfish (*Sebastes* spp.) in the northern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s

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ABSTRACT

Savenkoff, C., B. Morin, D. Chabot, and M. Castonguay. 2006. Main prey and predators of redfish (*Sebastes* spp.) in the northern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s. Can. Tech. Rep. Fish. Aquat. Sci. 2648: vi+23 pp.

We used results of mass-balance models to describe the changes in the structure and functioning of the northern Gulf of St. Lawrence ecosystem related to redfish (*Sebastes* spp.) for the mid-1980s, the mid-1990s, and the early 2000s. The net decrease in biomass of the demersal species in the early 1990s and the ensuing drop in predation led to an ecosystem structure dominated by small-bodied pelagic species and marine mammals. Redfish consumption largely decreased from the mid-1980s to the early 2000s. Large zooplankton, capelin (*Mallotus villosus*), and small zooplankton were the main prey consumed by redfish for each time period. There was a net decrease in total mortality and predation on redfish from the mid-1980s to early 2000s. Fishing mortality also decreased over the same time period as the redfish fishery in the Gulf has been under moratorium since 1995. Predation was the main cause of redfish mortality for each time period. The main predators of redfish were large cod (*Gadus morhua*) during the mid-1980s and harp seals (*Pagophilus groenlandicus*) and skates during the mid-1990s and early 2000s. Even though the proportion of redfish in the diet composition of each of these three predators was generally low, their predation could account for high percentages of total mortality on redfish. Cannibalism also appeared to be an important source of redfish mortality (between 10 and 15% of total mortality).

RÉSUMÉ

Savenkoff, C., B. Morin, D. Chabot, and M. Castonguay. 2006. Main prey and predators of redfish (*Sebastes* spp.) in the northern Gulf of St. Lawrence during the mid-1980s, mid-1990s, and early 2000s. Can. Tech. Rep. Fish. Aquat. Sci. 2648: vi+23 pp.

Nous avons utilisé les résultats de modèles d'équilibre de masse pour décrire les changements dans la structure et le fonctionnement de l'écosystème du nord du golfe du Saint-Laurent associés au stock de sébaste (*Sebastes* spp.) pour le milieu des années 1980, le milieu des années 1990 et le début des années 2000. La forte diminution des biomasses des espèces démersales au début des années 1990 et la chute résultante de leur prédation ont conduit à une structure de l'écosystème dominée par des petits poissons pélagiques et des mammifères marins. La consommation du sébaste a largement diminué depuis le milieu des années 1980 jusqu'au début des années 2000. Le grand zooplancton, le capelan (*Mallotus villosus*) et le petit zooplancton étaient les principales proies consommées par le sébaste à chaque période de temps. Il y a eu une forte diminution de la mortalité totale et de la prédation sur le sébaste depuis le milieu des années 1980 jusqu'au début des années 2000. La mortalité par la pêche a également diminué pendant la même période de temps du fait du moratoire imposé sur la pêche au sébaste depuis 1995. La prédation était la principale cause de mortalité du sébaste pour chaque période de temps. Les principaux prédateurs du sébaste étaient la grande morue (*Gadus morhua*) pendant le milieu des années 1980 et le phoque du Groenland (*Pagophilus groenlandicus*) et les raies pendant le milieu des années 1990 et le début des années 2000. Même si la proportion de sébaste dans l'alimentation de chacun de ces trois prédateurs était généralement faible, leur prédation pouvait représenter des pourcentages élevés de la mortalité totale du sébaste. Le cannibalisme apparaissait également comme une source importante de mortalité du sébaste (entre 10 et 15 % de la mortalité totale).

INTRODUCTION

Mass-balance models based on inverse methodology have been constructed to describe trophic interactions, ecosystem structure, and the effect of fishing in the northern Gulf of St. Lawrence ecosystem (Northwest Atlantic Fisheries Organization [NAFO] divisions 4RS; Figure 1) (Savenkoff et al. 2004a and submitted[1]). Three models have been constructed, corresponding to three different periods and states of this ecosystem. In the mid-1980s, groundfish stocks were considered healthy and were fished. The situation was very different in the mid-1990s: most large-bodied demersal fish populations had declined severely from the previous period and many stocks were protected by moratoria on direct fishing (CAFSAC 1994). For example, the biomasses of Atlantic cod (*Gadus morhua*), redfish (*Sebastes* spp.), and large demersals (mainly white hake [*Urophycis tenuis*], black dogfish [*Centroscyllium fabricii*], and Atlantic halibut [*Hippoglossus hippoglossus*]) were down 15-, 8-, and 4-fold, respectively (Morissette et al. 2003, Savenkoff et al. 2004b). The last model covers the early 2000s, after moratoria for cod were ended and fishing had resumed, albeit at very low levels compared to historic levels (Fréchet et al. 2003), even though demersal stocks showed no signs of recovery in the northern Gulf and most other areas (Rice and Rivard 2003).

The collapse of demersal fish stocks resulted in major changes in the structure and functioning of the northern Gulf ecosystem between the mid-1980s and early 2000s. (Savenkoff et al. 2004a and submitted). These were large-bodied piscivorous species that exerted strong predation pressures on many species of fish and invertebrates. Overfishing removed this functional group, which has not been replaced ten years after the cessation of heavy fishing. Marine mammals such as seals and cetacea were the top predators of many species during the mid-1990s, whereas marine mammals and small Greenland halibut were the dominant predators during the early 2000s. Predation by marine mammals on fish increased from the mid-1980s to early 2000s while predation by large fish on fish decreased.

In this report, we used results of the mass-balance models to present the effects of these ecosystem changes on the prey and predators of the redfish stock. Our results also enable us to evaluate the effects of fishing and predation on redfish for each time period.

MATERIAL AND METHODS

Data used in modelling

The data set covers a region of the northern Gulf of St. Lawrence (NAFO division 4RS) equivalent to a total area of 103,812 km^2 (Figure 1). The St. Lawrence Estuary was not included in the study. The nearshore region (depths < 37 m) was also excluded in the models, along with infra-littoral species such as American lobster (*Homarus americanus*), because this zone was not sampled by the research vessel survey and because exchanges between infra-littoral and mid- to off-shore zones are still poorly understood.

[1]: Savenkoff, C., Castonguay, M., Chabot, D., Bourdages, H., Morissette, L., and Hammill, M. O. Changes in the northern Gulf of St. Lawrence ecosystem estimated by inverse modelling: Evidence of a fishery-induced regime shift? Submitted for publication.

In this report, we used results of mass-balance models to describe the changes in the structure and functioning of the northern Gulf of St. Lawrence ecosystem related to redfish for the mid-1980s, the mid-1990s, and the early 2000s. Based on data availability and the ecological and commercial significance of the species, the whole-system model of the northern Gulf of St. Lawrence was divided into different functional groups or compartments (32 for the mid-1980s and mid-1990s, 31 for the early 2000s) representing the main pelagic, demersal, and benthic species present (Table 1). The model structure for the early 2000s differs slightly from that of the mid-1980s and mid-1990s due to ecological refinements (Savenkoff et al. 2005; Table 1). Details of the methods and data for the parameter estimates for each group as well as the modelling structure are given in Morissette et al. (2003) for the mid-1980s, Savenkoff et al. (2004b) for the mid-1990s, and Savenkoff et al. (2005) for the early 2000s. These three technical reports are available online at www.osl.gc.ca/cdeena/en/publications.shtml. In the "Redfish background" section below, we presented details of the input data for redfish only.

Inverse modelling

Inverse models use mass-balance principles and an objective least-squares criterion to estimate flows of organic matter or energy among components of an ecosystem and to generate a "snapshot" of the system at one moment in time (Vézina and Platt 1988; Savenkoff et al. 2004a). As opposed to traditional approaches, the ecosystem is considered as a whole, taking into account trophic interactions between all functional groups. Inverse methods provide a powerful tool to estimate ecosystem flows using limited data, straightforward mass balance, and metabolic constraints.

In inverse modelling, we assumed that there was no change in biomass during each studied time period and that net migration was zero (migration out of or into the study area, food intake of predators that are not part of the system, etc.). Under this steady-state assumption, the sum of inflows (consumption for each consumer group) is balanced by the sum of outflows (production, respiration, and egestion for each consumer group). Also, production was equal to the biomass lost to fishing, predation, and natural mortality other than predation (hereafter termed "other mortality causes"). Other mortality causes could include other natural causes of death such as disease or could reflect unsuspected processes occurring in the ecosystem, such as misreported catch (e.g., Savenkoff et al. 2004a), unsuspected migration, or other processes not accounted for in the model. For phytoplankton, the net (corrected for respiration) production must balance the sum of the outputs (phytoplankton mortality including the egestion term and consumption of phytoplankton). For the detritus group, the inputs (egestion and other natural causes of death for other groups) must balance the sum of the outputs (consumption of detritus, bacterial remineralization of detritus, and burial). As bacteria were considered part of the detritus, detritus were assumed to respire. Details of the model structure and method of solution for the different equations are given in Savenkoff et al. (2004a and submitted).

The models are useful in constraining observations into coherent pictures (Savenkoff et al. 2004a and submitted); however, since the number of flows to be solved exceeded the number of independent mass-balance relations (i.e., an underdetermined system), there is no unique solution to any model. Also, it remains that the results are sensitive to some choices we made regarding the modelling structure and that other valid solutions are possible. However, for each model presented in the next section, the final solution is always the mean of 30 iterations with random

perturbations of the input data (to a maximum of their standard deviations) and one solution without perturbation (the "initial solution") to provide an overall view of the ecosystem and to identify robust patterns. The estimated flows fell inside our *a priori* constraints and therefore were a reasonable "middle ground" description. Simulated inverse analyses have shown that the general flow structure of ecosystems can be recovered with these techniques, although the details can be inaccurate (Vézina and Pahlow 2003).

Redfish background

Redfish, also known as ocean perch or rosefish, occur on both sides of the Atlantic Ocean in cool waters (3° to 8°C) along the slopes of fishing banks and deep channels at depths of 100–700 m. Redfish distribution in the Northwest Atlantic ranges from west Greenland in the north to the Gulf of Maine in the south (Atkinson and Melteff 1987). Three species are currently recognized in the Northwest Atlantic, *Sebastes mentella* (Travin, 1951), *S. fasciatus* (Storer, 1854), and *S. norvegicus* (Ascanius, 1772), but the latter is relatively uncommon except on the Flemish Cap. *Sebastes mentella* generally occupies waters deeper than 250 m while *S. fasciatus* is usually found in shallower waters down to 300 m. The temperature preference in the Gulf of St. Lawrence (divisions 4RST + 3Pn and 4Vn from January to May) is between about 4.5 and 6.0°C. Redfish are lecithotrophic (larvae feeding exclusively on energy stored in yolk) and viviparous, and fertilization is internal. Mating occurs in the fall, and females carry the developing young until the spring when they are released from April to July. In all areas examined, *Sebastes mentella* release their young a month earlier than *S. fasciatus*. Redfish are slow growing and long lived: some specimens are estimated to be at least 80 years old. *Sebastes fasciatus* reaches a smaller size at age than *S. mentella* and growth is usually faster in southern areas than in northern areas; females also grow faster than males. Redfish generally take 8 to 10 years before being recruited to the commercial fishery at approximately 25 cm in length. These species have been commercially fished since the early 1950s, but a moratorium was imposed on redfish fishing in 1995 in the Gulf of St. Lawrence. Redfish in the Gulf of St. Lawrence were previously managed as NAFO divisions 4RST only. In 1991, a recommendation was made to modify the management units to consider the winter migration of redfish to the Cabot Strait area. Thus 3Pn4Vn (Jan. to May) were included with 4RST in 1993 to constitute the unit 1 stock (Atkinson and Power 1991).

In the Gulf of St. Lawrence, there have been three periods of intensive exploitation of redfish: from 1954 to 1960, the late 1960s to the early 1970s, and the early 1990s (Morin et al. 2001) (Figure 2). The second and third periods were closely related to the recruitment of one or two strong year-classes. After these three periods, landings fell rapidly from 77 000 t in 1992 to about 19 500 t in 1994, the last year that fishing was allowed. The high rate of exploitation, the low abundance of the stock, and the lack of any significant recruitment since the early 1980s have resulted in the current low stock size (Gascon 2003).

To estimate the magnitude of the trophic fluxes, the models require measurements or estimates of different parameters (input data) such as biomass, diet composition, catches as well as consumption and production rates for each group. Input data used in modelling and estimated fluxes for redfish for each period are summarized in Table 2. Several scenarios were tested for 1985–1987. Here, we used the estimates from the most realistic solution, the "misreporting solution," that included misreported catches of large cod (Savenkoff et al. 2004a). In this

solution, the catches of large cod have been increased by 30%, a level consistent with estimates of misreported cod catches in the northern Gulf in the mid-1980s (Savenkoff et al. 2004a). Some values were slightly different from data published in previous technical reports (Morissette et al. 2003, Savenkoff et al. 2004b, Savenkoff et al. 2005) due to model updates.

Catch (Table 2)

Commercial landings were estimated from NAFO landing statistics (NAFO 2003). In the northern Gulf, the mean annual total catch was 27,486 t or 0.26 t km^{-2} yr^{-1} (SD = 0.03 t km^{-2} yr^{-1}; range: 0.24-0.29 t km^{-2} yr^{-1}) during the 1985–1987 period, 1,731 t or 0.02 t km^{-2} yr^{-1} (SD = 0.04 t km^{-2} yr^{-1}; range: 0.00-0.05 t km^{-2} yr^{-1}) during the 1994–1996 period, and 767 t or 0.007 t km^{-2} yr^{-1} (SD = 0.001 t km^{-2} yr^{-1}; range: 0.007-0.008 t km^{-2} yr^{-1}) during the 2000–2002 period. The modelling catch estimates were 0.26, 0.02, and 0.007 t km^{-2} yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively.

Biomass (Table 2)

The *Lady Hammond* and CCGS *Alfred Needler* scientific surveys provided data from NAFO zones 4RS during the 1985–1987, 1994–1996, and 2000–2002 periods to estimate annual biomass (DFO, groundfish survey database, unpublished data). For redfish, length frequency data from each year were extrapolated to the whole northern Gulf area using the *PACES* software (Bourdages 2001). Total biomass was estimated each year by multiplying the abundance estimate for each length increment by the mean mass at length (derived from length–mass relationships) and summing the results. Average annual biomass estimates were 1,261,248 t or 12.15 t km^{-2} (SD: 2.46 t km^{-2}) for 1985–1987, 148,682 t or 1.43 t km^{-2} (SD: 0.62 t km^{-2}) for 1994–1996, and 110,976 t or 1.07 t km^{-2} (SD: 0.13 t km^{-2}) for 2000–2002.

Production (Table 2)

Due to the lack of reliable information on production (P) and total mortality (Z) for redfish in NAFO divisions 4RST, it was assumed that production was equivalent to biomass multiplied by natural mortality (M), plus catch (Allen 1971). Natural mortality (M) was assumed to be 0.125 yr^{-1} for redfish (Bundy et al. 2000). When the minimum and maximum biomass values were used for each period, we obtained production ranges of 0.61 to 3.65 t km^{-2} yr^{-1} (mean: 1.78 ± 2.15 t km^{-2} yr^{-1}) for 1985–1987, 0.12 to 0.32 t km^{-2} yr^{-1} (mean: 0.19 ± 0.15 t km^{-2} yr^{-1}) for 1994–1996, and 0.12 to 0.16 t km^{-2} yr^{-1} (mean: 0.14 ± 0.02 t km^{-2} yr^{-1}) for 2000–2002 (Table 2). The modelling production estimates for redfish were 2.48, 0.23, and 0.14 t km^{-2} yr^{-1} for 1985–1987, 1994–1996, and 2000–2002, respectively.

Consumption (Table 2)

FishBase was first used to estimate the annual food consumption to biomass ratio (Q/B) of redfish, assuming a water temperature of 3°C (Froese and Pauly 2002). This resulted in a Q/B of 2.100 yr^{-1}. Other sources of information on redfish consumption are available. Dolgov and Revetnyak (1990) estimated Q/B ratios for Barents Sea deep-water redfish (*Sebastes mentella*) that varied from a high of 6.0 yr^{-1} for fingerlings down to around 1.3 yr^{-1} for fish of 19 years of age. Since fingerlings and very young fish did not make up a significant part of the biomass, the mean Q/B of fish from 10 to 19 years of age was computed. This produced a mean Q/B ratio of 1.490 yr^{-1}. In another study on redfish from west Greenland, it was determined that daily rations were 0.46% and 0.86% of body mass for the autumn–winter and spring–summer periods, respectively (Pedersen and Riget 1992). These two values were averaged, which gave a mean of 0.66% body mass per day and was equivalent to a Q/B ratio of 2.409 yr^{-1}. On Georges Bank, the Q/B ratio for redfish was estimated at 7.970 yr^{-1} (Pauly 1989).

When the minimum and maximum biomass values and the different previous Q/B ratios were used, we obtained consumption ranges of 18.10 to 96.83 t km^{-2} yr^{-1} for 1985–1987, 1.57 to 17.14 t km^{-2} yr^{-1} for 1994–1996, and 1.38 to 9.39 t km^{-2} yr^{-1} for 2000–2002. Based on the mean production for each period and the minimum and maximum gross growth efficiency limits (GE, the ratio of production to consumption: 10–30%; Christensen and Pauly 1992), we obtained consumption values of 5.94 to 17.83 t km^{-2} yr^{-1} for 1985–1987, 0.63 to 1.90 t km^{-2} yr^{-1} for 1994–1996, and 0.47 to 1.41 t km^{-2} yr^{-1} for 2000–2002. However, assuming that these species would eat at least as much food as their biomass per year ($Q/B \geq 1$), the resulting lower and upper consumption limits used were 12.15 and 96.83 t km^{-2} yr^{-1} for 1985–1987, 1.43 and 17.14 t km^{-2} yr^{-1} for 1994–1996, and 1.07 and 9.39 t km^{-2} yr^{-1} for 2000–2002 (Table 2). The inverse solution estimated a consumption of 15.33 t km^{-2} yr^{-1} for 1985–1987, 1.46 t km^{-2} yr^{-1} for 1994–1996, and 1.14 t km^{-2} yr^{-1} for 2000–2002.

Diet composition (Table 3)

Stomach content data for redfish were available from 1993 to 1999 only. Redfish frequently regurgitate their stomach contents as a result of gas bladder inflation when retrieved from great depths. Some regurgitation may have taken place even when the stomach still contained some food, so analyses based on stomach fullness are not possible. However, we considered that the relative proportion of prey items in the stomachs, and the proportion of stomachs with food containing specific prey items, should both be representative. For each model, we distinguished two periods: (1) 1994–1996, which included winter, spring, and summer samples; and (2) 1993 and 1997–1999, the other years (hereafter termed the "other-years" period), which included spring and summer samples. Sampling was length-stratified and covered all the study area for all seasons, but redfish were only taken in the deep channels of the northern Gulf. To estimate a diet most representative of the entire year, average diets were calculated for each season (in % mass) and then averaged into a final diet using sample size (number of stomachs containing food) as a weighting factor (82, 420, and 158 for spring, summer, and winter 1994–1996 respectively; 181 and 382 for spring and summer of the other years). The most important prey items of redfish were shrimp, large zooplankton, and capelin for the 1994–1996 (94.2% of the diet) and other-years (97.2% of the diet) periods. The redfish diet from Bundy et al.

(2000), in which main prey items were large zooplankton (53.8%), small zooplankton (16.1%), and small planktivorous pelagics (24.5%), was also used. The overall mean diet composition combining these three sources of data, along with the minimum and maximum contribution of each group to redfish diet, are given in Table 3. The values calculated by inverse models for each modelled period are also given.

RESULTS

Main prey groups consumed by redfish

Redfish consumed thirteen prey groups at each period, although only three to four groups were important (> 5% in the redfish diet) (Figure 3). Large zooplankton, capelin (*Mallotus villosus*), and small zooplankton were the main prey for each time period (Figure 3). Large zooplankton includes organisms and species greater than 5 mm in length such as euphausiids (mainly *Thysanoessa raschii, T. inermis*, and *Meganyctiphanes norvegica)*, chaetognaths (mainly *Sagitta elegans*), hyperiid amphipods (mainly *Themisto libellula, Parathemisto abyssorum*, and *P. gaudichaudii*), jellyfish (cnidarians and ctenophores), mysids (mainly *Boreomysis arctica*), tunicates, and ichthyoplankton. The small zooplankton includes zooplankton less than or equal to 5 mm in length. Copepods, mainly *Calanus finmarchicus, C. hyperboreus*, and *Oithona similis*, are the most numerous small zooplankton in the study area. In our inverse models, we were not able to estimate the individual proportion of each species aggregated in large and small zooplankton groups consumed by redfish. According to the models, redfish consumption decreased from the mid-1980s to the early 2000s (from 15.3 ± 2.6 to 1.1 ± 0.2 t km^{-2} yr^{-1}; Figure 3) due to the decrease in redfish biomass (Table 2). Overall, the proportion of shrimp (mainly northern shrimp *Pandalus borealis*) in the diet composition of redfish increased from 4 to 27%, while the proportions of fish prey slightly decreased from 27 to 22%. These changes in the proportion of the different prey types ingested by redfish should be interpreted with caution because we used the same diet composition based mostly on stomach contents from the 1990s to constrain the three models. Differences in the estimated proportions of prey consumed by redfish were therefore related to mass conservation, trophic interactions among groups, and eco-physiological constraints specific to each time period modelled. It would be useful to resume a stomach sampling program for redfish to assess whether or not specific prey (e.g., shrimp) have become more important in their diet compared with the 1990s.

Role played by redfish in the northern Gulf ecosystem

When redfish biomass was high during the mid-1980s, redfish were among the main prey and predators in the northern Gulf ecosystem. Redfish biomass was much lower during the other two periods; as a result, redfish were no longer among the main prey or predator groups in the ecosystem. During the mid-1980s, capelin represented 57% of matter consumed within the ecosystem when planktonic and benthic invertebrate groups (lower trophic levels) were not considered (Figure 4). The other main prey groups were planktivorous small pelagics (e.g., herring and sand lance; 15%), redfish (8%), and shrimp (7%). There was a four-fold decrease in the matter consumed from the mid-1980s to mid-1990s (from 19.1 ± 3.0 to 4.8 ± 0.5 t km^{-2} yr^{-1};

Figure 4). During the mid-1990s, capelin accounted for 63% of matter consumed while the two other main prey groups were shrimp and planktivorous small pelagics (9% of matter consumed each). From the mid-1990s to early 2000s, there was an increase in the amount of matter consumed within the ecosystem (from 4.8 ± 0.5 to 7.3 ± 0.9 t km^{-2} yr^{-1}). The main prey was capelin (43% of all matter consumed) followed by shrimp (22%) and planktivorous small pelagics (14%).

During the mid-1980s, large cod were the main predators on fish prey (Figure 5). After large cod, redfish and capelin (via cannibalism) were the most important predators on fish. During the mid-1990s, the net decrease in biomass of the demersal species and the ensuing drop in predation coincided with an increase in marine-mammal biomass and predation. Cetaceans and seals became the main predators on fish. Predation by marine mammals on fish increased from the mid-1980s to early 2000s (from 1.54 ± 0.18 to 3.07 ± 0.73 t km^{-2} yr^{-1}) while predation by large fish on fish decreased (from 15.95 ± 2.98 to 2.18 ± 0.38 t km^{-2} yr^{-1}). Cetaceans and seals were still the main predators on fish, followed by small Greenland halibut during the early 2000s (Figure 5). Redfish was consumed by 13 to 14 predators during each time period.

Main causes of redfish mortality

Predation dominated the total mortality of redfish (63% of total mortality; Figure 6) during the mid-1980s. Other mortality causes represented about 27% of total mortality, while fishing accounted for 11%. Large cod was the main predator, causing 41% of the total mortality in redfish, whereas cannibalism accounted for close to 15% of total mortality. The proportion of redfish was 14 and 2%, respectively, in the diet compositions of large cod and redfish. Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.13, 0.02, and 0.05 yr^{-1}, respectively.

From the mid-1980s to mid-1990s, there was a ten-fold decrease in total redfish mortality (from 2.48 ± 0.55 to 0.23 ± 0.07 t km^{-2} yr^{-1}, Figure 6). Predation dominated total mortality even more (81%) in the mid-1990s while other mortality causes and fishing represented 11 and 8% of total mortality, respectively. Harp seals (*Pagophilus groenlandicus*) and skates had become the main predators of redfish, contributing to 30% and 19%, respectively, of total mortality (Figure 6). Cannibalism still accounted for close to 14% of total mortality for this species. The proportion of redfish was 7, 24, and 2%, respectively, in the diet compositions of harp seals, skates, and redfish. Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.13, 0.01, and 0.02 yr^{-1}, respectively.

Total redfish mortality still decreased from the mid-1990s (0.23 ± 0.07 t km^{-2} yr^{-1}) to the early 2000s (0.14 ± 0.04 t km^{-2} yr^{-1}). Predation accounted for 88% of total mortality while other mortality causes and fishing represented 7% and 5% of total mortality, respectively. Harp seals were the main predators of redfish (47% of total mortality; Figure 6). The proportion of redfish was 5% in the diet compositions of harp seals. Annual mortality rates for predation, fishing, and other mortality causes were estimated at 0.10, 0.01, and 0.01 yr^{-1}, respectively. Predation, fishing, and other mortality causes decreased in absolute values from the mid-1980s to the early 2000s (Figure 6).

DISCUSSION / CONCLUSION

The changes that occurred in the northern Gulf of St. Lawrence over the past 20 years were driven by human exploitation of selected species and would largely qualify as a fishery-induced regime shift. Overfishing in the early 1990s removed a functional group, large demersal species, which has not been replaced ten years after the cessation of heavy fishing (Rice and Rivard 2003). This has left only marine mammals as top predators in the 1990s and 2000s, although small Greenland halibut became important predators during the early 2000s (Savenkoff et al. submitted). The net decrease in the biomass of demersal species in the early 1990s led to an ecosystem structure dominated by small-bodied pelagic species and marine mammals in the northern Gulf.

Over this period, total catches decreased, and landings, at first dominated by long-lived piscivorous groundfish, consisted mostly of planktivorous pelagic fish and invertebrates in the more recent periods. This trend in fishing down the food web has unfortunately become widespread in fisheries throughout the northern hemisphere (Pauly et al. 1998). The near disappearance of catches of demersal species in recent years is responsible for this change in the trophic level of the catches. Reported cod and redfish landings accounted for 61 and 14%, respectively, of the total catches during the mid-1980s while forage fish and invertebrates represented only 21%. During the mid-1990s, reported cod and redfish landings accounted for only 1 and 4%, respectively, of the total catches while forage fish and invertebrates represented 90%. In the early 2000s, a few years after a limited cod fishery had resumed in the northern Gulf, cod catches increased to 11% of the total catches while redfish landings accounted for only 1% (redfish was still covered by a fishing moratorium). The remaining fisheries showed only minor changes (catches of forage fish and invertebrates: 85%).

A redfish multidisciplinary research program (1995–1999) was developed to examine aspects of the biology and fisheries of redfish and to develop a better understanding of these species in order to ensure long-term economic viability and sustainability of the fishery (Gascon 2003). The program has resulted in a wealth of valuable new information about redfish in the Northwest Atlantic. However, it remains unclear why demersal fish populations failed to recover following the cessation of directed fishing.

In the Gulf of St. Lawrence, strong redfish recruitment has been intermittent, occurring every 6–12 years. There were strong year-classes in 1946, 1956, 1958, 1970, and 1980 (Morin et al. 2004). Also, year-classes that were present in very large numbers at age 2 to 4 (based on research survey data: 1966, 1974, and 1988) were not found in subsequent years and never contributed significantly to the fishery. The factors responsible for the disappearance of these small immature redfish are unknown. Possible causes were reviewed (Gascon 2003), including fishing mortality due to by-catches in the shrimp fishery and natural mortality due to poor environmental conditions or predation. None of them could be clearly associated with the observed variations in recruitment. Information from the shrimp fishery in the Gulf at the beginning of the 1990s showed a high amount of discards in 1992 (Gascon 2003). With the introduction of the Nordmore grid in the shrimp fishery in 1993, the amount of juvenile redfish discards decreased significantly (Gascon 2003). Also, low survival of *S. mentella* larvae could be related to the cold temperature regime in the Gulf at the end of the 1980s (DFO 2000). Preliminary analyses of existing data from the Gulf of St. Lawrence suggested that successful redfish year-classes correspond to particular climatic conditions that may influence not only the

physical conditions in which the larvae are produced but also the quantity and quality of their preferred prey.

Even though this report does not deal with redfish larvae, it enables us to evaluate the relative impact and interplay of the main mortality causes (fishing, predation, and natural mortality other than predation) on juvenile and adult redfish in the northern Gulf of St. Lawrence during three time periods that cover the collapse of demersal species and the management regulations that followed. In the northern Gulf, the models indicated that there was a net decrease in total mortality and predation on redfish from the mid-1980s to early 2000s. Fishing mortality also decreased during the same time period as the Gulf redfish fishery has been under moratorium, since 1995. However, both annual mortality rates for predation and fishing remained fairly stable across all three time periods (on average 0.12 and 0.1 yr^{-1}, respectively), even though redfish were under moratorium during two of these time periods. Predation was the main cause of redfish mortality in the northern Gulf for all time periods. Large cod during the mid-1980s and harp seals and skates during the mid-1990s and early 2000s were the main predators of redfish. Even though the proportion of redfish in the diet composition of each of these three main predators was generally low (large cod: 2–14%; harp seals: 4–8%; skates: 18–24%), predation could account for high percentages of total mortality (e.g., large cod: 41% during the mid-1980s, harp seals: 47% during the early 2000s; Figure 6). However, this picture could have been a little bit different if the 1990–1992 period had been analyzed since juveniles of the 1988 year-class were very abundant in the northern Gulf: their role as prey or predators in the ecosystem would have been important.

Cannibalism also appeared to be an important source of redfish mortality. Population models of exploited fish stocks include a cannibalism component that tends to depress recruitment at high stock sizes (Hilborn and Walters 1992). Savenkoff et al. (submitted) showed that cannibalism by large cod was the main source of mortality on small cod (50%) during the mid-1980s and still had a significant impact during the mid-1990s and early 2000s (25 and 13% of total mortality on small cod, respectively), even though small cod constituted a minor component of the diet of large cod (at most 6% of the diet). For redfish, cannibalism represented between 11 and 15% of total mortality at each time period. The proportion of redfish in the diet composition of redfish was also low (at most 2% of the diet).

The reasons for the collapse and lack of recovery of depleted demersal fish stocks during the moratoria (and after it for cod) are complex and no single factor can explain all observations. Monitoring programs (fishery statistics, commercial sampling, and research surveys) allow a fair assessment of the past and current status of the stocks. Ecosystem models could become powerful new tools for fishery management. The model results already provide valuable information on the impact of fishing relative to the effects of predation and natural mortality other than predation on the fish and invertebrate communities.

Modelling of large marine ecosystems is still in its infancy. Our current models, even with 30 compartments, still represent simplifications of the trophic interactions in the northern Gulf of St. Lawrence. The validity of any conclusion regarding the ecosystem being studied depends on the input data (and the confidence that we have in them). This work is the result of a huge effort to assemble data on the biological characteristics of species occurring in the northern Gulf of St. Lawrence at three time periods. Even though most of the data are good estimates for the 4RS ecosystem, some input values are rough estimates only, meaning that these values are assembled from different literature sources and not from independently measured parameters. Some errors in parameter estimates could significantly alter the system's biomass budget, especially for the

most important species of the ecosystem, or produce a totally different balanced solution. Overall, even though the model is not a perfect representation of reality, it is probably as good as it can be with the information available. This illustrates the need for further work to improve the input parameters in order to enhance the quality of future modelling efforts. Information on the effects of fishing and predation on redfish stock in the Gulf of St. Lawrence has to continue to be investigated to improve management practices.

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See the CDEENA web site at http://www.osl.gc.ca/cdeena/en/accueil.shtml.

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Table 1. Functional groups used in modelling in the northern Gulf of St. Lawrence for each time period.

Group name	Main species
Cetaceans[a]	Mysticeti (baleen whales): *Balaenoptera physalus*, *Balaenoptera acutorostrata*, *Megaptera novaeangliae*
	Odontoceti (toothed whales): *Lagenorhynchus acutus*, *L. albirostris*, *Phocoena phocoena*
Harp seals[b]	*Pagophilus groenlandicus*
Hooded seals[b]	*Cystophora cristata*
Grey seals[c]	*Halichoerus grypus*
Harbour seals[c]	*Phoca vitulina*
Seabirds	*Phalacrocorax carbo*, *P. auritus*, *Larus delawarensis*, *L. argentatus*, *L. marinus*, *Sterna hirundo*, *S. paradisaea*, *Cepphus grylle*, *Oceanodroma leucorhoa*, *Morus bassanus*, *Rissa tridactyla*, *Uria aalge*, *Alca torda*, *Fratercula arctica*
Large Atlantic cod (> 35 cm)	*Gadus morhua*
Small Atlantic cod (≤ 35 cm)	*Gadus morhua*
Large Greenland halibut (> 40 cm)	*Reinhardtius hippoglossoides*
Small Greenland halibut (≤ 40 cm)	*Reinhardtius hippoglossoides*
American plaice	*Hippoglossoides platessoides*
Flounders	*Limanda ferruginea*, *Glyptocephalus cynoglossus*, *Pseudopleuronectes americanus*
Skates	*Amblyraja radiata*, *Malacoraja senta*, *Leucoraja ocellata*
Redfish	*Sebastes mentella*, *Sebastes fasciatus*
Large demersal feeders	*Urophycis tenuis*, *Melanogrammus aeglefinus*, *Centroscyllium fabricii*, *Anarhichas* spp., *Cyclopterus lumpus*, *Lycodes* spp., Macrouridae, Zoarcidae, *Lophius americanus*, *Hippoglossus hippoglossus*
Small demersal feeders	*Myoxocephalus* spp., *Tautogolabrus adspersus*, *Macrozoarces americanus*, juvenile large demersals
Capelin	*Mallotus villosus*
Sand lance[d]	*Ammodytes* spp.
Arctic cod[e]	*Boreogadus saida*

Table 1. Cont.

Group name	Main species
Large pelagic feeders	*Squalus acanthias*, *Pollachius virens*, *Merluccius bilinearis*
Piscivorous small pelagic feeders	*Scomber scombrus*, piscivorous myctophids and other mesopelagics, *Illex illecebrosus*, piscivorous juvenile large pelagics
Planktivorous small pelagic feeders	*Clupea harengus*, planktivorous myctophids and other mesopelagics, *Scomberesox saurus*, *Gonatus* spp., planktivorous juvenile large pelagics
Shrimp[f]	*Pandalus borealis*, *P. montagui*, *Argis dentata*, *Eualus macilentus*, *E. gaimardii*
Crabs[g]	*Chionoecetes opilio*, other non-commercial species (e.g., *Hyas* spp.)
Echinoderms	*Echinarachnius parma*, *Strongylocentrotus pallidus*, *Ophiura robusta*
Molluscs	*Mesodesma deauratum*, *Cyrtodaria siliqua*
Polychaetes	*Exogone hebes*
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly *Calanus finmarchicus*, *C. hyperboreus*, and *Oithona similis*), tunicates < 5 mm, meroplankton, heterotrophic protozoa (flagellates, dinoflagellates, and ciliates)

Table 1. Cont.

Group name	Main species
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *C.* spp., *Leptocylindrus minimus*, *Thalassiosira nordenskioeldii*, *T.* spp., *Fragilariopsis* spp., and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, and Prymnesiophytes
Detritus	Sinking particulate or_anic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, and bacteria)

[a]: Cetaceans were separated into two groups for the early 2000s: the mysticeti (baleen whales) and the odontoceti (toothed whales).

[b]: Harp and hooded seals were grouped in the early 2000s due to a combination of limited data and a weak trophic role in the mid-1980s and mid-1990s ecosystems for hooded seals.

[c]: Grey and harbour seals were grouped in the early 2000s due to a combination of limited data and a weak trophic role in the mid-1980s and mid-1990s ecosystems for harbour seals.

[d]: Included in the planktivorous small pelagic feeders in the early 2000s due to very low biomass for sand lance in the early 2000s (biomass: 0.003 t km^{-2} vs 2.398 and 0.120 t km^{-2} for the mid-1980s and mid-1990s, respectively).

[e]: Included in the capelin group in the early 2000s due to a combination of limited data and a weak trophic role in the mid-1980s and mid-1990s ecosystems for Arctic cod.

[f] Shrimp were separated into large (≥ 22 mm carapace length, CL; mainly female *P. borealis*), and small (< 22 mm CL; *P. borealis* juveniles and males and other shrimp species) shrimp in the early 2000s.

[g]: Crabs were separated into small (≤ 45 mm carapace width, CW) and large (> 45 mm CW) crabs in the early 2000s.

Table 2. Observed mean, minimum, and maximum values for redfish estimated using inverse modelling for each time period. Modelling estimates are also shown. Inverse modelling does not estimate biomass. Values used in data equations or as upper and lower limit constraints are indicated in boldface[1].

Parameter	1985–1987	1994–1996	2000–2002
Mean catch (t km^{-2} yr^{-1})	**0.26**	**0.02**	**0.007**
Minimum catch (t km^{-2} yr^{-1})	0.24	0.00	0.007
Maximum catch (t km^{-2} yr^{-1})	0.29	0.05	0.008
Modelling estimated catch (t km^{-2} yr^{-1})	0.26	0.02	0.007
Mean biomass (t km^{-2})	12.15	1.43	1.07
Minimum biomass (t km^{-2})	10.31	1.05	0.92
Maximum biomass (t km^{-2})	14.95	2.15	1.18
Mean production (t km^{-2} yr^{-1})	1.78	0.19	0.14
Minimum production (t km^{-2} yr^{-1})	**0.61**	**0.12**	**0.12**
Maximum production (t km^{-2} yr^{-1})	**3.65**	**0.32**	**0.16**
Modelling estimated production (t km^{-2} yr^{-1})	2.48	0.23	0.14
Mean consumption t km^{-2} yr^{-1})	54.49	9.29	5.23
Minimum consumption (t km^{-2} yr^{-1})	**12.15**	**1.43**	**1.07**
Maximum consumption (t km^{-2} yr^{-1})	**96.83**	**17.14**	**9.39**
Modelling estimated consumption (t km^{-2} yr^{-1})	15.33	1.46	1.14

[1]: Some of the input data were introduced directly into the models as data equations. The data equations attempt to fix the value of certain flows or combinations of flows. These included mean values (e.g., catch) estimated from field studies and values available only as point estimates (no variance) or with low observed values (e.g., <0.5%) and low uncertainty (e.g., SD < 0.6%). The production and consumption values that were not estimated from local field studies as well as the diet proportions with higher values (e.g., >0.5%) were incorporated as constraints.

Table 3. Diet composition of redfish used in modelling of the northern Gulf for each time period. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

					1985–1987	1994–1996	2000–2002
Prey	Mean	± SD	Min	Max	Est	Est	Est
Small cod	**0.1**	0.1	0.0	0.2	0.0	0.1	0.1
Redfish	1.1	1.7	**0.0**	**2.4**	2.4	2.3	1.4
Small demersals	0.9	1.3	**0.1**	**1.9**	1.0	0.1	0.1
Capelin	10.3	14.4	**0.7**	**21.1**	21.1	21.0	17.1
Pisci. small pelagics	**0.3**	0.4	0.0	0.5	0.2	0.3	0.3
Plank. small pelagics	12.2	17.3	**0.0**	**25.9**	2.6	0.3	3.5
Shrimp	31.1	41.7	**3.5**	**62.4**	3.9	6.1	27.0
Molluscs	**0.0**	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes	**0.0**	0.0	0.0	0.0	0.0	0.0	0.0
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.0	0.0	0.0
Large zooplankton	36.3	21.7	**23.1**	**53.8**	52.7	53.7	37.0
Small zooplankton	7.8	11.1	**0.4**	**16.1**	16.1	16.1	13.6
Total	100.0		27.8	184.3	100.0	100.0	100.0
TRN	12						

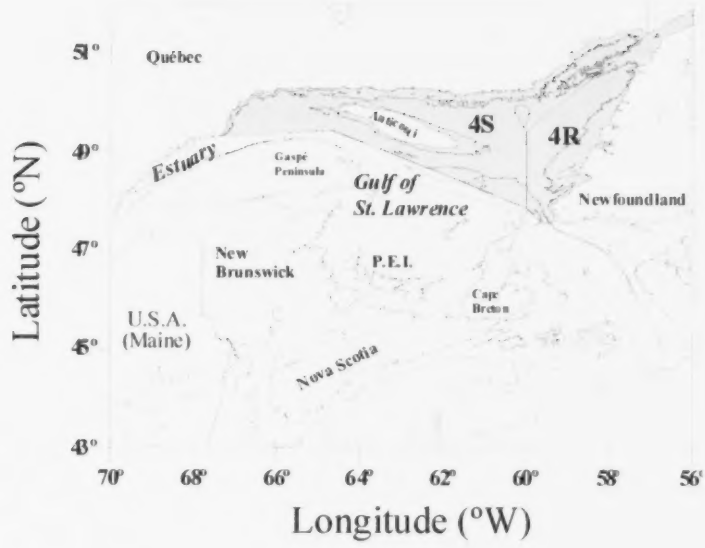

Figure 1. Northern Gulf of St. Lawrence (NAFO divisions 4RS) equivalent to a total area of 103,812 km^2.

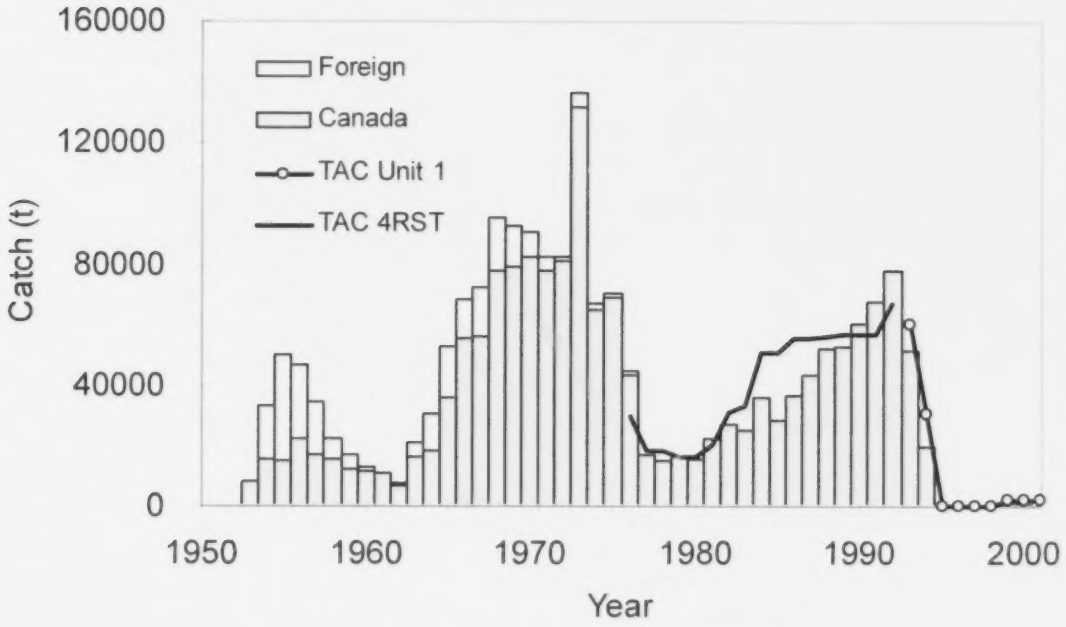

Figure 2. Historical commercial landings of redfish in the Gulf of St. Lawrence. TAC: total allowable catch.

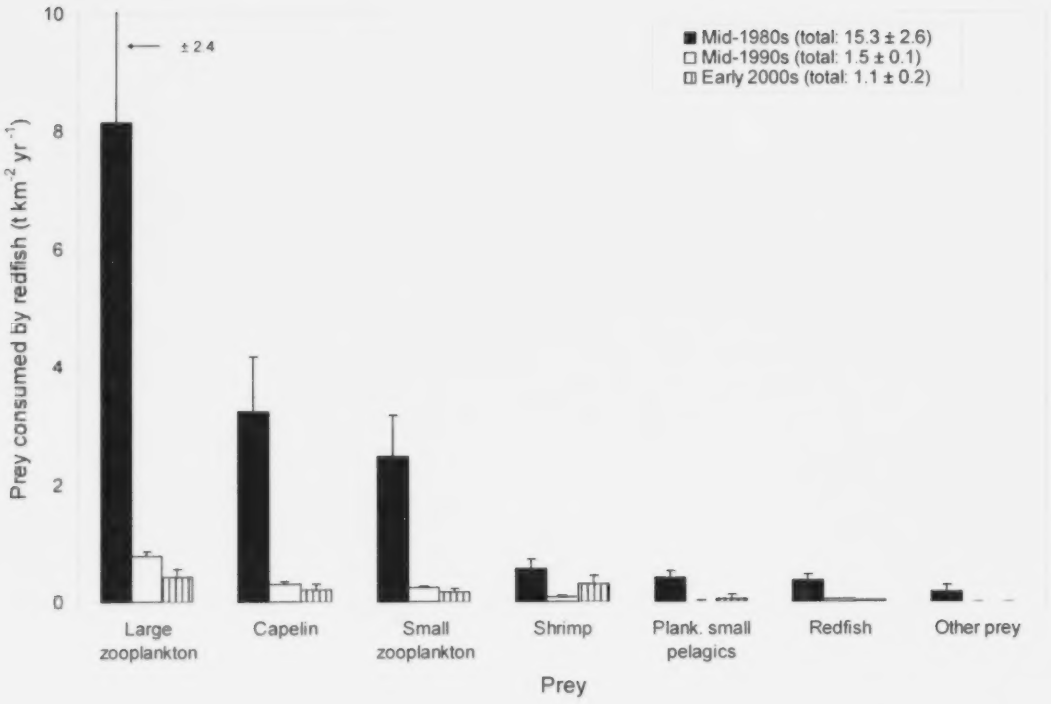

Figure 3. Prey consumed by redfish estimated for each time period. Total consumption by redfish for each time period (in t km^{-2} yr^{-1}) is shown in the legend. Bars show mean values and SD.

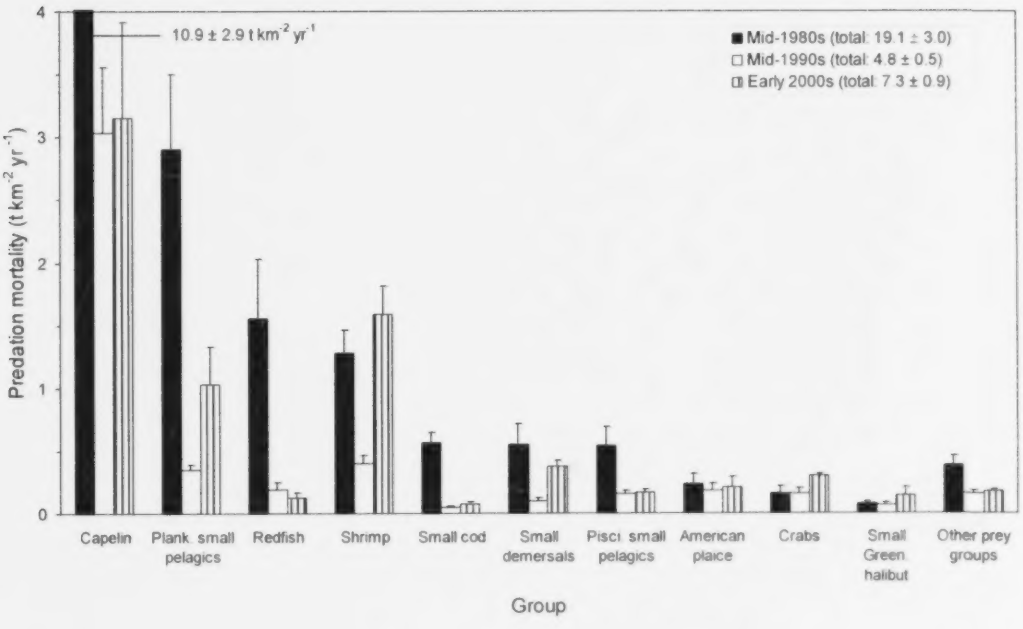

Figure 4. Predation mortality on different groups showing the main vertebrate and crustacean prey consumed in the northern Gulf of St. Lawrence for each time period. The other prey groups accounted for 2% (flounders: 0.8%, large demersals: 0.6%, and other species: < 0.3% each) during the mid-1980s, 3% (large cod: 1.0%, large demersals and skates: 0.7% each, and other species: < 0.4% each) during the mid-1990s, and 2% (large cod: 0.9%, large demersals: 0.6%, and other species: < 0.3% each) during the early 2000s. Bars show mean values and SD.

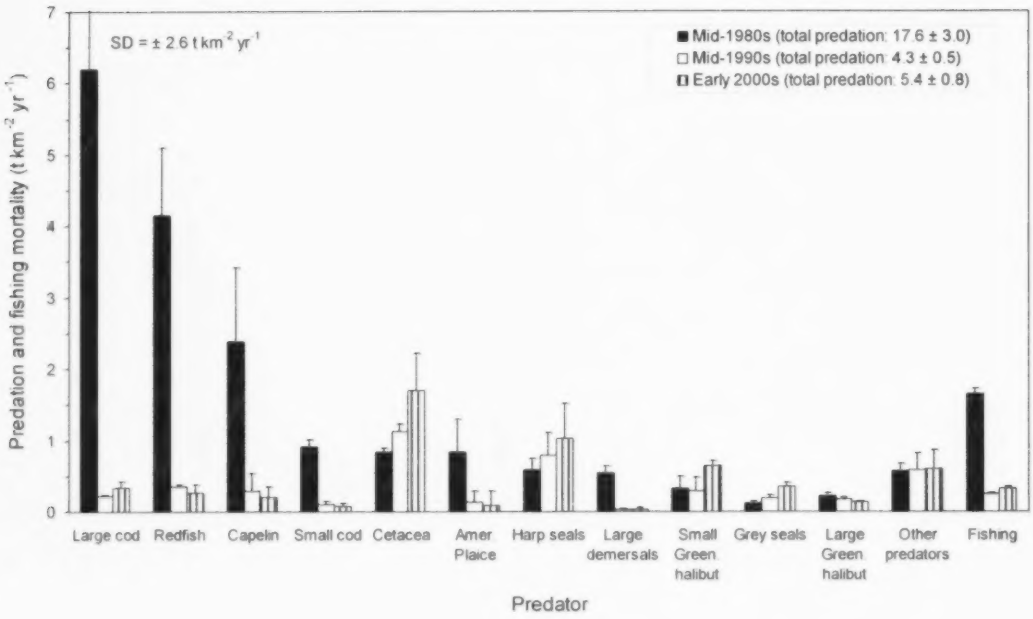

Figure 5. Predation mortality on fish by different groups showing the main predators in the northern Gulf for each time period. For comparisons, fishing mortality on fish is also included. The other predators accounted for 3% (seabirds: 0.8%, small demersals: 0.6%, and other species: < 0.4% each) during the mid-1980s, 13% (seabirds: 5.3%, piscivorous small pelagics: 3.3%, small demersals: 2.0%, skates: 1.8%, and other species: < 0.2% each) during the mid-1990s, and 10% (seabirds: 3.5%, piscivorous small pelagics: 2.9%, and other species: < 1.2% each) during the early 2000s. Bars show mean values and SD.

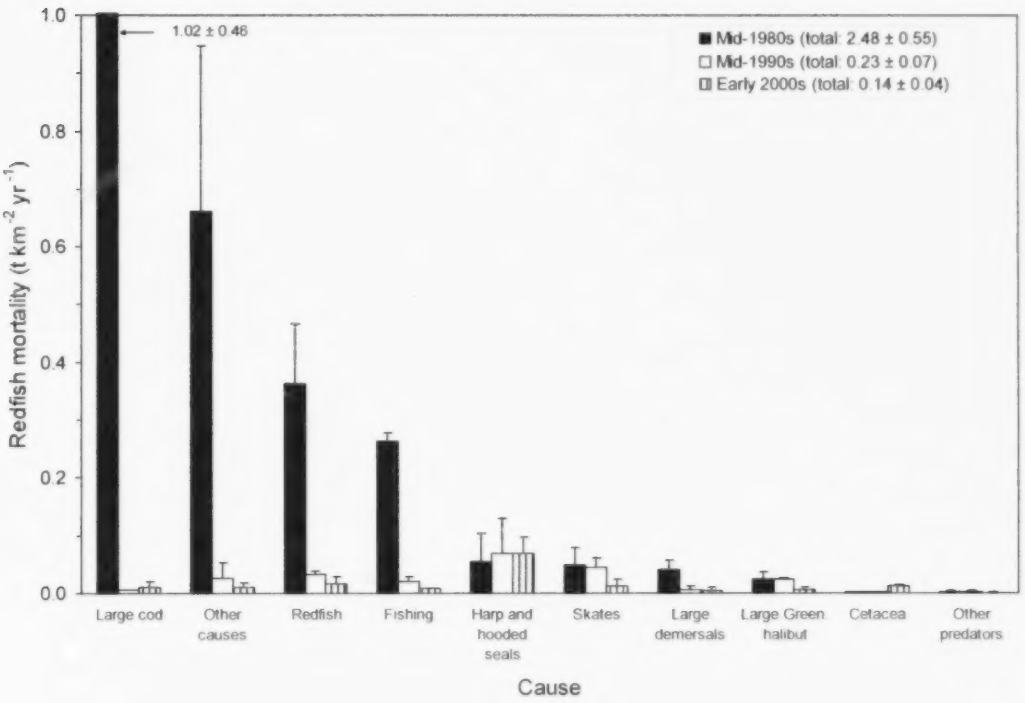

Figure 6. Main causes of redfish mortality (fishing, predation, and natural mortality other than predation; i.e., other mortality causes) estimated for each time period. Bars show mean values and SD.